FLORISTIC ANALYSIS OF THE SOUTHWESTERN UNITED STATES

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Abstract.—A study was made of the distributions of native, terrestrial, vascular plants occurring in 50 local floras from throughout the Basin and Range and Colorado Plateau physiographic provinces of the southwestern United States. The objectives of the study were to objectively define and describe the floristic elements—assemblages of species with roughly coincident geographic distribution—occurring in the southwestern United States and to determine what such assemblages reveal about the floristic history of the region.

The total flora (native, terrestrial species only) of the Southwest is estimated at 5,458 species, 77% of which were recorded in 1 or more of the local floras. Nearly 22% of these species are endemic to the study region. A majority of the species were found to be relatively rare. The average range of a species included only 4 floras, and 90% of the species were recorded from 11 or fewer floras; only 81 species (1.5%) were recorded from 50% or more of the floras. Trees constitute 2% of the regional flora and have the widest average distribution; perennial herbs constitute 59% of the flora and have the most restricted distributions.

Factor analysis was used to identify seven floristic elements for the region: a Great Basin element, a Mojavean element, a Colorado Plateau element, a Chihuahuan element, an Apachian element, and a Mogollon element. This factor analysis solution was shown to satisfy criteria of interpretability and consistency. The Mojavean, Colorado Plateau, and Apachian elements are believed to be autochthonous. The other four elements show high overlap in species composition with one or more adjacent regions.

Each floristic element is mapped to show its geographic form and distribution. Analysis of these maps shows how the existence of objectively defined floristic elements is not contradictory to either the individualistic view of the distribution of a species or local continuity of vegetation and flora.

The rarity of the majority of species and the clear association of floristic elements with rather narrowly circumscribed Holocene environments suggests that many Southwestern species have migrated little and are of rather recent, probably postglacial origin. Geographic "principles" derived from the distribution patterns of relatively few, widespread, dominant, usually woody species may not be applicable to entire, regional floras.

Plant geographers have long recognized that plant species can be grouped on the basis of similarities among their geographic distributions. Such floristic groups have generally been termed "geographical elements" by European phytogeographers (Stott 1981, Cain 1947). The same concept is embodied in such terms as "natural floristic areas" (Raup 1947), "floristic assemblage" (Cain 1944), "floristic group" (Gleason and Croquist 1964), "areal types" (Whittaker and Niering 1964), "categories of geographic origin" (Stebbins 1982), or "directional classes" (Meyer 1978) of American authors. The term *element* is used uncritically in the American literature as a synonym for taxon or taxa.

A concept related to that of floristic assemblages is that of floristic or biotic provinces. Provinces in the sense of Dice (1943) are reasonably discrete areas with characteristic physiography, climate, vegetation, flora, and fauna. There may be a one to one correspondence between floristic groups and floristic provinces (e.g., Gleason and Cronquist 1964), in which case the floristic group is the characteristic flora of the floristic province. More often floristic groups are conceived as assemblages of variable and often overlapping areal extent, including a few wide-ranging types and many more narrowly defined types. A good example is the set of "areal types" used by Whittaker and Niering (1964) in their analysis of the flora of the Santa Catalina Mountains of southern Arizona. Included are widespread and overlapping "temperate," "western," "northern," and "southwestern" types along with more restricted and largely discrete "Sonoran," "Rocky Mountain," "Plains," "Madrean," and "Chihuahuan" types.

This chaos in terminology regarding floristic assemblages is a consequence of the inadequate empirical and theoretical basis for such concepts in the American tradition. Gleason (1926) challenged the validity of the organismic concept of associations as applied to vegetation by F. E. Clements and argued further that each species has its own individualistic environmental requirements and migrational history. It should follow, therefore, that each community of species is unique and any attempt to identify repeatable associations must be highly subjective. The "individualistic concept" and the related "continuum concept" have been accepted by most American plant ecologists (McIntosh 1967).

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The ideas of Gleason were very broadly applied to plant geography by Mason (1947) and Cain (1944, 1947). Mason (1947) invoked the individualistic nature of the species and the principles of past migrations of species (as revealed in the fossil record) to argue against the existence of persistent and recognizable floras. Cain (1947) believed that floristic elements could be recognized only relative to the particular area under investigation and not as a universal system of floristic regions. He linked the ideas of floristic groups and plant association types, and went on to argue against the objective recognition of association types, implicitly casting doubt on the objective recognition of floristic assemblages of any form.

The current attitude toward floristic assemblages is well illustrated in a statement by Johnston (1977:356):

> "Recurrent distribution patterns" may simply be the result of intuitive (but in this case unfortunate?) tendencies to lump and generalize, in the way the eye tends to connect totally unrelated star-clusters into meaningless but "recognizable" patterns in the night sky.

A recent text on biogeography (Brown and Gibson 1983) discusses the association/continuum conflict but makes no reference to the problem of floristic elements.

If each plant species is uniquely and independently distributed, and therefore recognition of floristic assemblages must be inherently arbitrary and subjective, why have so many phytogeographers nevertheless recognized such groups? Can phytogeographical elements be described more objectively and, if so, how can they be reconciled with individualistic concepts and what do they mean in terms of the evolutionary histories of their species? The objective of this paper is to answer these questions through a floristic analysis of vascular plant distributions recorded in local floras from the southwestern United States.

METHODS

Study Region

The study region includes the Colorado Plateau Physiographic Province and the Basin and Range Physiographic Province north of the U.S.-Mexico International Boundary, both as mapped by Hunt (1967) (Fig. 1). This region is bounded by the Sierra Nevada and southern California transverse ranges on the west; by the Columbia Plateau on the north; and by the Rocky Mountains and southern Great Plains on the east. Only the southern boundary is artificial. This region will be referred to simply as the Southwest.

The majority of the region lies between the two great Western mountain systems—Sierra Nevada on the west and Rocky Mountains to the east. The entire region is arid to semiarid. The Great Basin section of the Basin and Range Province experiences hot summers, cold winters, and mostly winter precipitation. The southeastern portion of the Basin and Range Province is at the opposite end of the climatic spectrum for the region, with hot summers, mild winters, and mostly summer precipitation. The most arid portion of the region centers around the lower Colorado River Valley.

The study region has generally been recognized as a natural one by biogeographers. One of the earliest formal treatments is that of Dice (1943) and a recent one is that of Cronquist (1982). Both recognize a semiarid natural region lying between the Sierra Nevada and the Rocky Mountains that extends into northern Mexico. Cronquist's Great Basin Province essentially includes Dice's Artemisian and Navahonian provinces; Cronquist's Sonoran Subprovince is composed of Dice's Mohavean and Sonoran provinces; and their Chihuahuan regions are similar. The principal difference is that there is nothing in Cronquist's treatment that corresponds closely to Dice's Apachian Province of the uplands of southeastern Arizona, southwestern New Mexico, and northwestern Sonora.

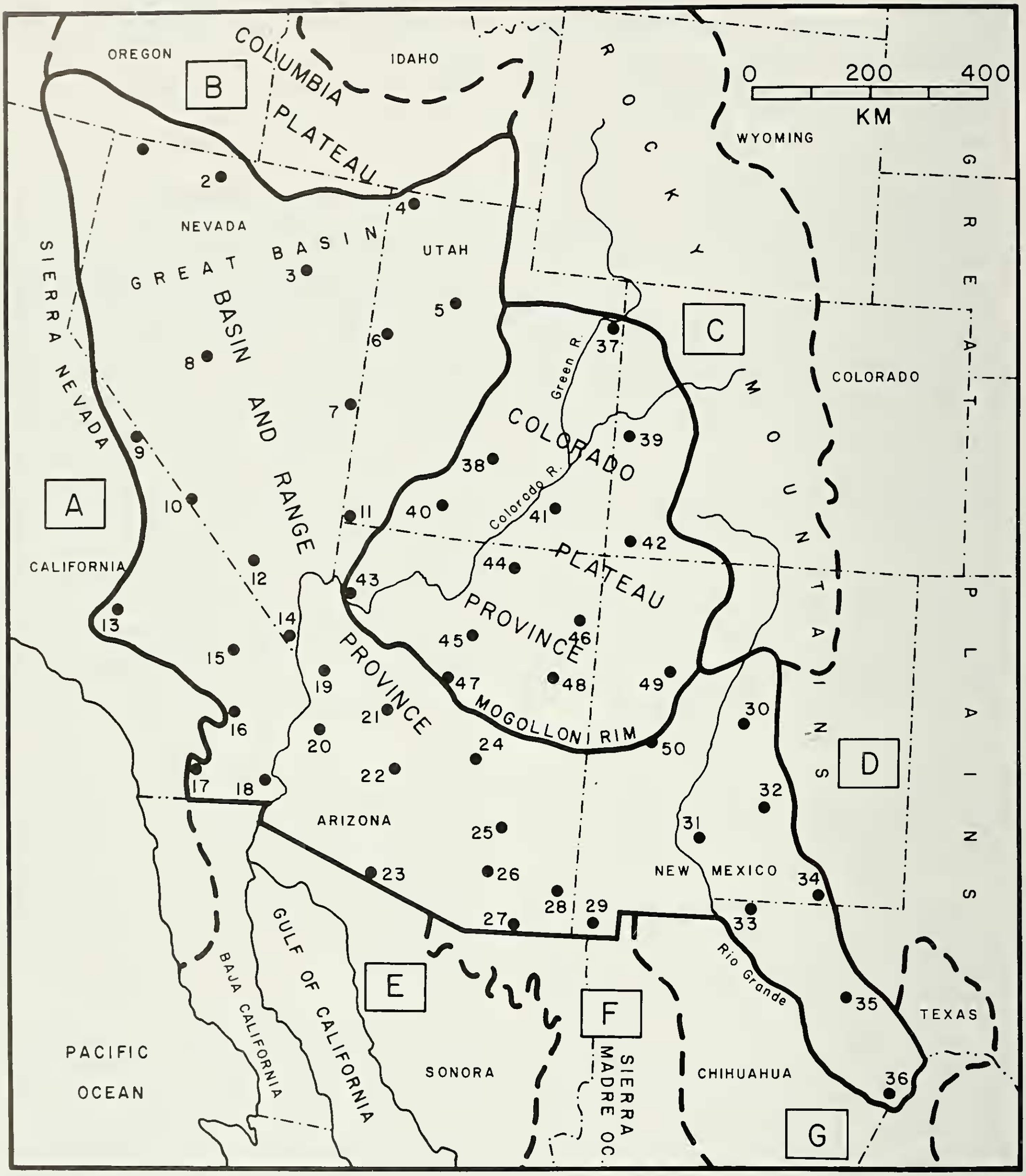


Fig. 1. Map of study region, Southwestern United States. Numbers refer to local floras listed in Table 1; letters in boxes refer to peripheral regions listed in Table 6.

Data Base

Fifty local floras from the Southwest were examined (Table 1). These floras represent a systematic sample of the regional southwestern flora and were selected to provide as thorough and uniform coverage of the study region as possible (see Fig. 1).

Complete bibliographic citations for 33 of the 50 local floras can be found in Bowers' (1982) annotated bibliography. Flora 42 is based both on the publication referenced in Bowers (1982) and on an unpublished checklist distributed by Natural Bridges National Monument. Flora 13 consists of those plants listed by Twisselman (1967) as occurring in

Table 1. Southwestern local floras used in floristic analysis. Map numbers refer to map locations in Figure 1.

Map location	Flora designation	Number of species	Reference
1	Sheldon National Wildlife Refuge	489	Rogers & Tiehm (1979)
2	Santa Rosa Mountains	318	Bowers (1982)
3	Ruby–East Humboldt Mountains	507	Lewis (1971)
4	Raft River Mountains	295	Bowers (1982)
5	Stansbury Mountains	476	Taye (1983)
6	Deep Creek Mountains	395	Bowers (1982)
7	Wheeler Peak area	380	Bowers (1982)
8	Toiyabe Mountains	440	Bowers (1982)
9	White Mountains (California-Nevada)	677	Lloyd & Mitchell (1973)
10	Grapevine Mountains	463	Kurzius (1981)
11	Beaver Dam Mountains	489	Bowers (1982)
12	Spring Range (Charleston Mountains)	603	Bowers (1982)
13	Eastern Kern County	368	Twisselman (1967)
14	Newberry Mountains	385	Holland (1982)
15	Granite Mountains	376	Thorne et al. (1981)
16	Joshua Tree National Monument	534	National Park Service (1973)
17	Western Colorado Desert Region	441	Clemons (1984)
18	Eastern Imperial County	227	McLaughlin & Bowers (unpublished)
19	Hualapai Mountains Planning Unit	623	Bowers (1982)
20	Harcuvar Planning Unit	491	Bowers (1982)
21	Skull Valley Planning Unit	488	Bowers (1982)
22	White Tank Mountains	304	Bowers (1982)
23	Organ Pipe Cactus National Monument	477	Bowers (1982)
24	Sierra Ancha Experimental Forest	655	Bowers (1982)
25	George Whittell Wildlife Preserve (Aravaipa Canyon)	398	Bowers (1982)
26	Saguaro National Monument, Rincon Mountain Unit	799	Bowers (unpublished)
27	Mule Mountains	387	Wentworth (1982)
28	Chiricahua National Monument	619	Bowers (1982)
29	Animas Mountains	620	Bowers (1982)
30	Manzano Mountains	349	Bowers (1982)
31	Jornado Experimental Range	493	Bowers (1982)
32	White Mountains (New Mexico)	895	Bowers (1982)
33	Hueco Tanks State Park	315	Worthington (1980)
34	Carlsbad Caverns—Guadalupe Mountains	543	Bowers (1982)
35	Davis Mountains	461	Sikes and Smith (1975)
36	Big Bend National Park	751	Warnock (1967)
37	Dinosaur National Monument	304	Bowers (1982)
38	Capitol Reef National Monument	402	Bowers (1982)
39	Colorado National Monument	302	Bowers (1982)
40	Bryce Canyon National Park	402	Buchanan & Graybosch (1982)
41	Natural Bridges National Monument	298	Bowers (1982), National Park Service (no date)
42	Mesa Verde	333	Bowers (1982)
43	Lower Grand Canyon area	250	Bowers (1982)
44	Navajo National Monument	252	Bowers (1982)
45	Wupatki National Monument	178	Bowers (1982)
46	Canyon de Chelly National Monument	396	Bowers (1982)
47	Oak Creek Canyon and vicinity	507	Bowers (1982)
48	Petrified Forest National Park	277	Bowers (1982)
49	Mount Taylor	274	Bowers (1982)
50	Datil Mountains	483	Bowers (1982)

the arid shrub, creosote bush, and shadscale scrub portions of eastern Kern County, California. Flora 17 consists of those plants listed by Clemons (1984) as occurring in the Vallecito, Carrizo, and Borrego floristic areas of eastern San Diego County, California. Floras 18 and 26 are from projects in progress.

The number of species listed in these local floras varies from a low of 178 to nearly 900 species. The species numbers given in Table 1 are in every case lower than the numbers given in the original reports, since several classes of species were not included in the present analysis:

a. Introduced species.
b. Strict aquatics, i.e., floating, submerged, and emergent plants of permanent lotic habitats (ponds, lakes, reservoirs, cattle tanks, etc.)
c. Synonyms at the species level.
d. Species listed by authors as "likely" to occur in their areas.

Aquatic species were excluded because of their limited value in comparative geographic studies. Such species tend to be very widespread but are relatively uncommon in dry regions, depending on the occurrence of suitable (often man-made) habitats. Kartesz and Kartesz (1980) and Welsh et. al (1981) were used to achieve consistency and uniformity in nomenclature and to identify synonymous plant names. In the remainder of this paper, flora of the study region will refer to the native, vascular, terrestrial flora as defined above.

In addition to recording the presence of species in each of the 50 local floras, manuals and checklists for the region (Holmgren and Reveal 1966, Cronquist et al. 1972, 1977, 1984, Kearney and Peebles 1969, Martin and Hutchins 1980, Munz 1968, Correll and Johnston 1970) were consulted to determine what additional species occur in the Southwest. Finally, again using regional manuals, I recorded occurrences of all southwestern species in each of seven adjacent or peripheral regions (see Fig. 1): (A) Pacific region (roughly equivalent to the California floristic province), (B) Columbia Plateau, (C) Rocky Mountain region, (D) Great Plains, (E) Sonoran Desert region, (F) Sierra Madre region, taken here as the area in northern Mexico between the Sonoran and Chihuahuan deserts, and (G) Chihuahuan Desert region. The resulting lists of southwestern species occurring in these peripheral regions were used as floras in the data analysis (see below) to examine the relationships between the Southwest flora and that of the peripheral regions, and to distinguish allochthonous from autochthonous elements.

Data Analysis

Similarities in the species composition of the 50 local floras and seven peripheral regions were examined using factor analysis. Factor analysis is a family of ordination techniques used to examine the pattern and structure of large data matrices. Factor analysis has long been used in sociological and geographic studies, and its applications for plant ecology have been discussed by Goodall (1954) and for phytogeography by Jardine (1972). Since it is essentially a nonhierarchical clustering procedure, factor analysis is a particularly appropriate tool for examining floristic affinities (Jardine 1972).

Factor analyses are of two basic types. Consider a matrix that lists the presences of s species (rows) in n floras (columns). A Q-mode analysis would examine the relationships in an s x s matrix of correlations or similarities among the s species; an R-mode analysis would examine the relationships in an n x n matrix of correlations or similarities among the n floras. Ideally one would prefer to perform a Q-mode analysis to investigate floristic affinities, but two problems arise: there is no suitable coefficient or similarity index available to correlate species ranges *when most of the species are very rare*; and available factor analysis programs are limited to ~100 variables (species in this case), a number smaller than the smallest local flora used in this study.

I therefore used an R-mode analysis based on similarity indices among the floras and peripheral regions. The R-mode and Q-mode solutions should agree whenever clear-cut patterns actually exist in the data (Bryant et al. 1974). The similarity index used was that of Otsuka (as given in Simpson 1980):

$$IS_{Otsuka} = C_{ij}/(A_iB_j)^{1/2}$$

where:

A_i = number of species in flora i;
B_j = number of species in flora j;
C_{ij} = number of species common to floras i and j.

Since IS_{Otsuka} can take only positive values between 0 and 1, the analysis used here is, in the terminology of Pielou (1984), one using standardized but noncentered data. With data in this form, the first several factors are usually unipolar, i.e., all or nearly all the factor loadings (see below) are of the same sign, all positive or all negative. Furthermore, there are as many unipolar factors as there are qualitatively different clusters of data points (Pielou 1984).

Table 2. Statistical summary of the native, terrestrial flora of the Colorado Plateau and Basin and Range provinces of the southwestern United States.

Taxonomic group	Families	Genera	Species	Endemic species no.	Endemic species %
Ferns and fern allies	9	24	120	3	(2.5)
Gymnosperms	3	7	36	2	(5.6)
Monocotyledons	10	136	723	63	(8.7)
Dicotyledons	105	827	4579	1119	(24.4)
Totals	127	994	5458	1187	(21.7)

The factoring program used was that of Nie et al. (1975). I used principal components factor extraction with orthogonal (varimax) rotation, probably the most commonly used factoring technique in ecological studies. Several aspects of the analysis were altered later to check on the consistency of the solution (see below).

RESULTS

Description of the Flora

The flora of the study region is summarized in Tables 2–6. A total of 4,185 species were recorded from the 50 local floras; 1,273 additional species native to the study region were identified from the literature. The estimated total regional flora (5,458 species) is probably somewhat conservative, since the flora of the intermountain region in Utah and Nevada is still being compiled and monographed. The sample of species in the 50 local floras, however, probably represents at least 70%–75% of the regional flora.

Table 2 lists total species and endemic species by major taxonomic group. Within the study region, 21.7% of the species are endemic. Most of the endemic species are dicotyledons, and, in fact, nearly a quarter of the dicotyledons are endemic. The proportion of endemics in the study region is much lower than that in the California floristic province to the west (47.7%) but higher than that of other continental areas including Alaska (5.9%), Texas (9.0%), or the northeastern United States (13.5%) (Raven and Axelrod 1978). There is a rather high ratio of species per genus (5.5) in the Southwest, similar again to that of the California floristic province (5.6) and higher than for most other continental areas (3.0–4.0) (Raven and Axelrod 1978).

The most common families and genera within the study region are listed in Table 3. Commonness as used in this paper refers to ubiquity rather than abundance (Preston 1948), although ubiquitous taxa are also usually abundant (Hengeveld and Haeck 1982, Brown 1984). The Asteraceae, which is the largest family, accounting for 17.1% of the total species in the flora, is also the most common family, with 78.6 species/flora. Poaceae is the second most common family even though it is represented by more than 100 fewer species than the Fabaceae, the third most common family. The families Fabaceae, Brassicaceae, Scrophulariaceae, Boraginaceae, Polygonaceae, and Cactaceae are characteristic families of the region in that they have both a large number of species and a high proportion (>25%) of their species endemic within the region. The five most common genera—*Eriogonum, Astragalus, Cryptantha, Penstemon*, and *Phacelia*—also have a high proportion of endemic species. Several large genera common within but not characteristic of the region, including *Carex, Juncus*, and *Salix*, are mostly found in relatively mesic habitats.

The frequency distribution for the 5,458 species occurring in the Southwest is shown in Figure 2. The average number of floras per species is 4.07. Only 81 species (1.5%) were recorded from one-half or more of the local floras (Table 4). Most of these widespread species have several subspecific taxa within the region, indicating that they are genetically variable species. The widespread species listed in Table 4 are found throughout most of western North America. The vast majority of species in the region, however, are rare. Nearly two-thirds of the species are recorded from three or fewer floras.

The distribution patterns of southwestern species, as revealed by their occurrence in the 50 local floras examined, are probably reliable evidence for the rarity of most species in this

TABLE 3. Commonest families and genera of native, terrestrial plants in the Colorado Plateau and Basin and Range provinces.

	Total	Species per	Endemic species	
Taxon	species	flora	number	%
10 MOST COMMON FAMILIES:				
Asteraceae	932	78.6	213	(22.9)
Poaceae	359	42.5	22	(6.1)
Fabaceae	493	28.2	154	(31.2)
Brassicaceae	208	16.6	66	(31.7)
Scrophulariaceae	276	16.3	114	(41.3)
Boraginaceae	161	13.2	52	(32.3)
Polygonaceae	172	12.8	73	(42.4)
Polemoniaceae	144	11.8	37	(25.7)
Rosaceae	110	11.2	23	(20.9)
Cactaceae	111	9.7	33	(29.7)
20 MOST COMMON GENERA:				
Eriogonum	120	9.4	64	(53.3)
Astragalus	189	7.4	111	(58.7)
Cryptantha	79	6.0	39	(49.9)
Penstemon	118	5.3	70	(59.3)
Phacelia	77	5.2	35	(45.5)
Carex	97	5.0	3	(3.1)
Muhlenbergia	48	4.8	7	(14.6)
Opuntia	36	4.7	7	(19.4)
Erigeron	72	4.7	29	(40.3)
Artemisia	22	3.8	1	(4.5)
Juncus	26	3.8	0	(0)
Chamaesyce	40	3.6	6	(15.0)
Senecio	50	3.6	9	(18.0)
Gilia[1]	46	3.5	14	(30.4)
Bouteloua	19	3.4	1	(5.2)
Brickellia	36	3.4	12	(33.3)
Oenothera[2]	29	3.3	6	(20.7)
Castilleja	45	3.2	13	(28.9)
Lupinus	57	3.2	13	(22.8)
Salix	28	3.2	1	(3.6)

[1] Excluding *Ipomopsis*, *Leptodactylon*.
[2] Excluding *Calyophus*, *Camissonia*.

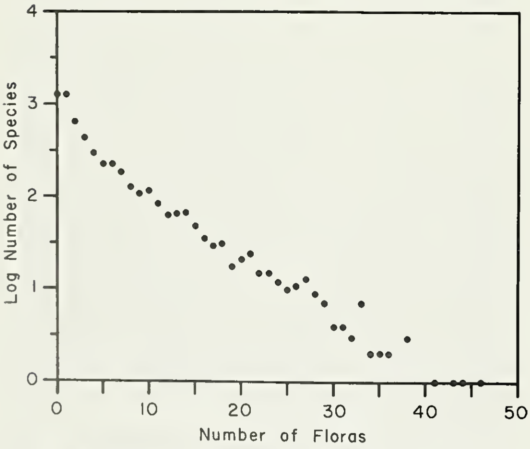


Fig. 2. Frequency distribution showing numbers of species occurring in 0–50 local floras from the southwestern United States.

region. Although I use the term *local* in reference to the floras, most of the floras used in this analysis cover rather extensive areas. Many of the floras are for small to large mountain ranges, national parks, and other areas that encompass a diversity of habitats. Within the boundaries covered by each flora there undoubtedly occur habitats suitable for many species not known to occur in the floras. Even if every species occurred on the average in one additional flora, it would not greatly change the statistics of species distributions; yet it would increase the size of each local flora by ~110 species. It is unlikely that 100 species (on the average) could be added to each local flora, even through very extensive further collection.

The composition of the flora by life form is summarized in Table 5. Trees and shrubs, though widely distributed, constitute only 14.2% of the total flora. Cacti and succulents

Table 4. Most commonly encountered species in 50 local floras from the southwestern United States.

Species[1]	Subspecific taxa[2]	% of floras	Species	Subspecific taxa	% of floras
Artemisia ludoviciana	7	92	*Astragalus lentiginosus*	37	56
Sitanion hystrix	2	88	*Plantago patagonica*	3	56
Descurainia pinnata	12	86	*Agropyron trachycaulum*	4	56
Rhus trilobata	6	82	*Populus tremuloides*	0	56
Erigeron divergens	2	76	*Comandra umbellata*	3	56
Atriplex canescens	3	76	*Castilleja linearifolia*	0	56
Aristida purpurea[3]	4	76	*Achillea millefolium*	11	54
Gutierrezia sarothrae	2	72	*Ceratoides lanata*	2	54
Mentzelia albicaulis	2	72	*Chenopodium fremontii*	2	54
Poa fendleriana	3	70	*Juncus arcticus*[4]	3	54
Mimulus guttatus	6	70	*Phoradendron juniperinum*	2	54
Vulpia octoflora	3	68	*Mirabilis multiflora*	3	54
Salix exigua	0	68	*Bromus carinatus*[3]	0	54
Conyza canadensis	3	66	*Koeleria cristata*	0	54
Linum lewisii	3	66	*Ipomopsis aggregata*	4	54
Oenothera caespitosa	8	66	*Amelanchier utahensis*	2	54
Bouteloua curtipendula	2	66	*Datura inoxia*	0	54
Senecio douglasii	3	66	*Celtis reticulata*	0	54
Oryzopsis hymenoides	2	66	*Baccharis glutinosa*	0	52
Holodiscus dumosus	2	66	*Senecio multilobatus*	0	52
Chrysothamnus nauseosus	20	64	*Cryptantha pterocarya*	4	52
Lappula redowskii	2	64	*Erysimum capitatum*	6	52
Sporobolus cryptandrus	0	64	*Lepidium lasiocarpum*	4	52
Opuntia phaeacantha	10	62	*Aristida adscensionis*	3	52
Sporobolus airoides	0	62	*Juncus ensifolius*[3]	2	52
Stephanomeria pauciflora	2	62	*Ranunculus cymbalaria*	3	52
Echinocereus triglochidiatus	8	62	*Nicotiana trigonophylla*	0	52
Helianthus annuus	0	60	*Chrysothamnus viscidiflorus*	5	52
Leucelene ericoides	0	60	*Pinus ponderosa*	3	50
Erioneuron pulchellum	0	60	*Pseudotsuga menziesii*	2	50
Rosa woodsii	4	60	*Gutierrezia microcephala*	0	50
Cercocarpus montanus	7	58	*Amaranthus blitoides*	0	50
Populus fremontii	2	58	*Artemisia tridentata*	3	50
Erigeron pumilus	6	58	*Stipa comata*	2	50
Draba cuneifolia	3	58	*Gilia sinuata*	0	50
Allionia incarnata	0	58	*Clematis ligusticifolia*	3	50
Bouteloua gracilis	2	58	*Fallugia paradoxa*	0	50
Castilleja chromosa	2	58	*Salix gooddingii*	0	50
Artemisia dracunculus	2	56	*Physalis hederifolia*	2	50
Brickellia californica	2	56	*Verbena bracteata*	0	50
Symphoricarpos oreophilus	2	56			

[1] Nomenclature follows Kartesz and Kartesz (1980) except where otherwise footnoted.
[2] Number of subspecific taxa listed in Kartesz and Kartesz (1980).
[3] *sensu* Cronquist et al. (1977).
[4] *sensu* Hultén (1968).

(mostly Agavaceae) make up 3.3% of the flora; annuals constitute 23.5%, a relatively high proportion. Perennial herbs, by far the largest group (58.9%), are the least widely distributed of the life forms listed in Table 5. Among herbaceous plants, species of Poaceae are relatively widespread (5.9 floras/species). Many species of the large genera characteristic of the region are rather uncommon, e.g., *Astragalus* (2.0 floras/species), *Penstemon* (2.2 floras/species), *Cryptantha* (3.1 floras/species), *Erigeron* (3.2 floras/species), *Phacelia* (3.4 floras/species), and *Gilia* (3.8 floras/species).

The number of southwestern species extending into the seven peripheral regions are listed in Table 6. These numbers imply nothing about directions of migration; rather they show only the overlap in species composition between the Southwest and adjacent regions. A species occurring in the Southwest and another region(s) may be: primarily southwestern, barely entering the peripheral region(s); primarily distributed in the peripheral region(s), barely entering the Southwest; or common in both the Southwest and one or more peripheral regions. The greatest overlap

TABLE 5. Summary of flora by life form.

Life form	No. species	Floras/Species
Trees	109	8.79
Shrubs	667	4.92
Perennial herbs	3,217	3.65
Annual herbs	1,285	4.24
Cacti and succulents	180	4.09
Total	5,458	4.06

TABLE 6. Species shared between Southwest and adjacent regions. Letters refer to map locations in Figure 1.

	Species occurring in Southwest	
Peripheral region	Number	Percent of total
A. Pacific region	1,544	28.3
B. Columbia Plateau region	1,224	22.4
C. Rocky Mountain region	1,479	27.1
D. Great Plains region	1,297	23.8
E. Sonoran region	847	15.5
F. Sierra Madre region	1,215	22.3
G. Chihuahuan region	1,119	20.5

occurs with the Pacific peripheral region, the least with the Sonoran Desert peripheral region. Two types of species appear to account for much of the overlap: species of disturbed or weedy habitats, and species of relatively mesic habitats.

Factor Analysis Solution

In principal components analysis the n variables are expressed in terms of n principal components (factors). By convention, only those factors with eigenvalues >1 (i.e., those factors accounting for at least 1/n of the variation in the data) are retained for rotation to the final solution. Nine such factors were extracted in this analysis. The 8th and 9th factors were bipolar with eigenvalues -1 and could not be simply interpreted. The 1st through 7th factors are depicted in Figures 3–9; they account for 55.4% of the variation in the data.

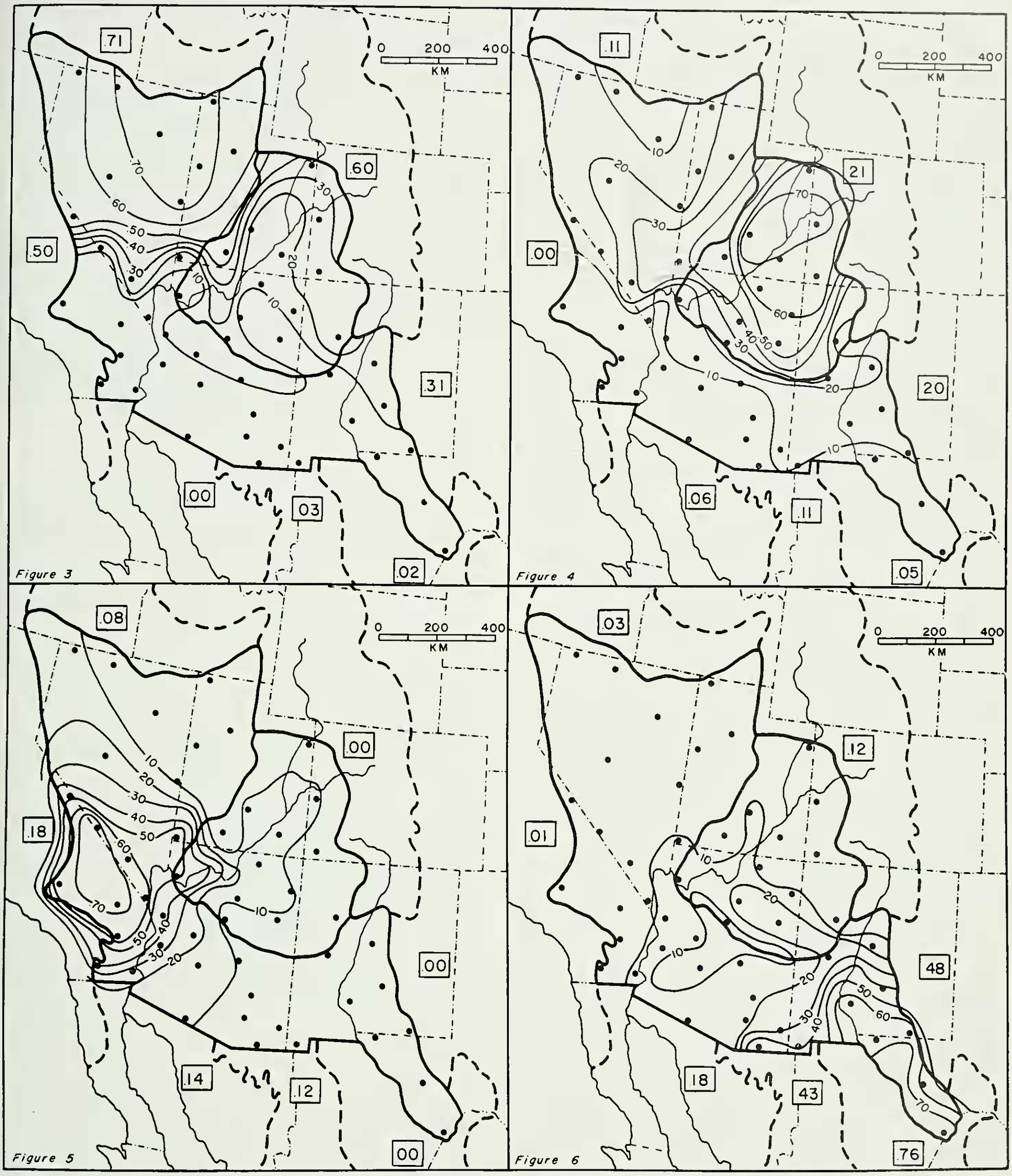
The maps of Figures 3–9 were prepared by plotting the factor loadings for each flora and drawing contours or isolines to show areas of approximately equal factor loadings. Factor loadings are the correlations between the floras and the factors. For this particular analysis, the factor loadings can be interpreted as similarity indices between the floras and the factors. The loadings for the peripheral regions are shown in the boxes on Figures 3–9.

Factor analysis to date has not been used extensively in biogeography, despite its potential ability to simplify complex data sets. Apparently, a major reason for this is that both authors and readers often must engage in some rigorous mental gymnastics to interpret the "meaning" of factors when there is considerable sampling error in the data or when patterns among the variables are in fact weak. Compared to most kinds of ecological data, there is relatively little error in determining which species occur in a particular area of limited extent. If the results of the factor analysis can be mapped, the interpretation should be straightforward—either there are simple, reasonable, and easily understood geographical patterns associated with each factor or there are not.

The factors mapped in Figures 3–9 are geographically meaningful. Each shows high similarity with relatively few adjacent local floras. From these centers of high similarity, the magnitude of factor loadings declines more or less continuously in all directions. In form the mapped factors are reminiscent of the "noda" of Poore (1955). Each factor is most strongly represented in a single section of the study region, and these areas are fairly well delimited. The factors clearly identify what areas within the Southwest show higher than average overlap in species composition between local floras. It seems to me that these seven factors can be interpreted readily as seven floristic elements in the traditional sense, that is, as clusters or centers of roughly coincident species ranges.

Most of the seven floristic elements correspond to natural areas that have been recognized in the past on more subjective grounds. I will discuss each briefly before proceeding to a discussion of the conceptual and theoretical basis for recognizing floristic elements.

1. GREAT BASIN ELEMENT.—Factor 1 (Fig. 3) has high loadings with floras in the Great Basin section of the Basin and Range physiographic province. This element shows a distinct representation in the eastern portion of the Colorado Plateau as well as a recognizable extension into the Mogollon Rim area of central Arizona. The element declines in importance most rapidly toward the south in southern Nevada. Beatley (1975) discusses the topographic and climatic factors in this latter area that are correlated with the transition from Great Basin to Mojave Desert vegetation.



Figs. 3–6: 3, Plots of loadings for factor 1—Great Basin floristic element. 4, Plot of loadings for factor 2—Colorado Plateau floristic element. 5, Plot of loadings for factor 3—Mojavean floristic element. 6, Plot of loadings for factor 4—Chihuahuan floristic element.

The Great Basin element is strongly correlated with the flora of the Columbia Plateau peripheral region to the north. Both are regions of sagebrush desert and conifer-forested mountain ranges. The Great Basin element is also strongly correlated with the Rocky Mountain region to the east and the Pacific region to the west—primarily the Sierra Nevada portion—both of which have probably contributed species to the Great Basin. The factor loading with the Rocky Mountain region is the higher of the two, suggesting that the contribution from there may have been greater than that from the Sierra Nevada, as noted previously by Harper et al. (1978).

2. COLORADO PLATEAU ELEMENT.—The second factor (Fig. 4) is clearly associated with the Colorado Plateau. Its greatest representation is in the northern portion of the Colorado Plateau about the confluence of the Green and Colorado rivers. The element extends beyond the limits of the Colorado Plateau into the southeastern Great Basin. Its most abrupt attenuation occurs along the southern boundary of the Colorado Plateau in the Mogollon Rim area.

Unlike the Great Basin element, the Colorado Plateau element is not strongly correlated with any of the peripheral regions. The Colorado Plateau is also an area of relatively high endemism (Fig. 10). The high incidence of endemics and the low similarities with peripheral regions identify the Colorado Plateau element as an autochthonous element.

3. MOJAVEAN ELEMENT.—The third factor (Fig. 5) is centered about the Mojave Desert region of southeastern California, northwestern Arizona, and southern Nevada. The Mojavean element, like the Colorado Plateau element, is weakly correlated with all peripheral regions, including the Sonoran Desert region. The rapid attenuation of the element to the west, where it meets the California floristic province, is notable. The Mojave Desert region has the highest frequency of endemic species in the Southwest (Fig. 10). This element is clearly autochthonous.

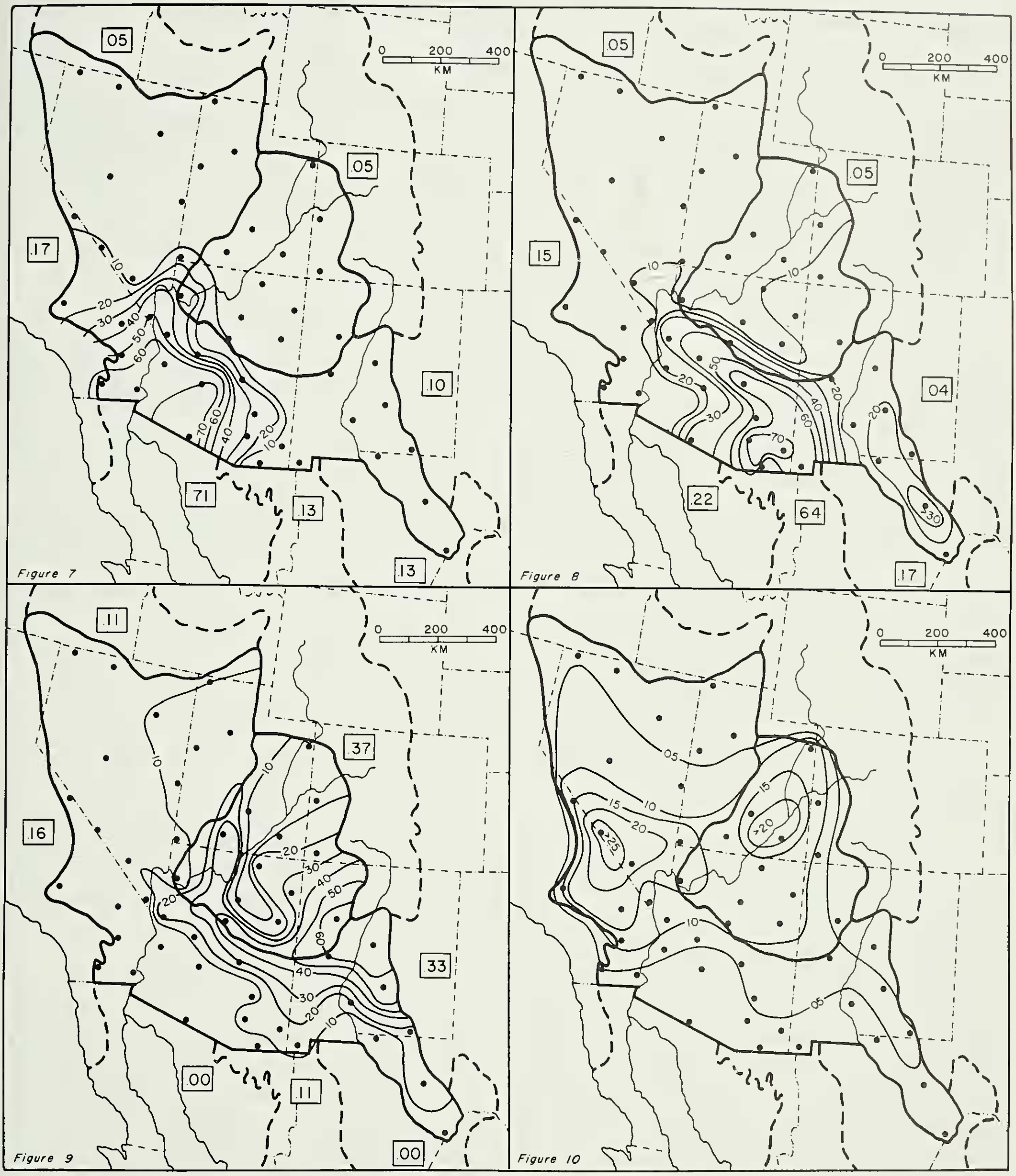
4. CHIHUAHUAN ELEMENT.—The fourth factor (Fig. 6) is identifiable as a Chihuahuan element, located in the Chihuahuan Desert area of Trans-Pecos Texas in the extreme southeastern portion of the study region. It extends up the Rio Grande Valley and into southeastern Arizona. In the latter region species with Chihuahuan affinities are frequently associated with limestone substrates (Whittaker and Niering 1968, Wentworth 1982). The Chihuahuan element is strongly correlated with the flora of the Chihuahuan peripheral region and is an extension of the flora of that region. The Chihuahuan element is also moderately correlated with the floras of the Plains and Madrean peripheral regions.

5. SONORAN ELEMENT.—The fifth factor (Fig. 7) is concentrated in southwestern Arizona and the Colorado Desert area of extreme southeastern California. It is highly correlated with the flora of the Sonoran Desert peripheral region and weakly correlated with all other peripheral regions.

The four desert elements recognized—Great Basin, Mojavean, Chihuahuan, and Sonoran—correspond very closely to the four desert regions of the same names recognized by Shreve (1942). In fact, the formal analysis presented here nicely confirms Shreve's impressions based on vegetation and flora. More recent interpretations that would include the Mojave Desert as a subdivision of the Sonoran Desert (Cronquist 1982; Turner 1982) are not supported. Floristic evidence favors retention of the Mojave Desert as a biogeographic entity distinct from the Sonoran Desert to the south.

6. APACHIAN ELEMENT. Factor 6 (Fig. 8) occurs primarily in southeastern Arizona and southwestern New Mexico. It can be termed an Apachian element in the sense of Dice (1943). The Apachian element extends all along the southern boundary of the Colorado Plateau along the Mogollon Rim into northwestern Arizona. An extension can easily be recognized in Trans-Pecos Texas and southern New Mexico east of the Rio Grande.

It is not clear from an analysis of floras from north of the International Border whether this element is largely autochthonous or allochthonous. The element could be centered within the mountainous region of southeastern Arizona, southwestern new Mexico, and northeastern Sonora, the Apachian Biotic Province of Dice (1943), or it could be a northern extension of a broader floristic element centered in the Sierra Madre Occidental of southeastern Sonora, southwestern Chihuahua, and northwestern Durango, the Sierra Madre Occidental Biotic Province of Goldman and Moore (1945). Two local floras from northwestern Mexico provide additional data. White (1948) prepared a large flora (927 native, terrestrial species) for the Rio de Bavispe region of extreme northeastern Sonora, including the Sierra del Tigre, often considered an outlying section of the Sierra Madre. Maysilles (1959) examined the flora (506 native terrestrial species) of the pine forests of western Durango in the central Sierra Madre. I have calculated the similarities between these two Mexican floras and five floras with high loadings on factor 6 (Table 7). The Bavispe flora shows high similarity with



Figs. 7–10: 7, Plot of loadings for factor 5—Sonoran floristic element. 8, Plot of loadings for factor 6—Apachian floristic element. 9, Plot of loadings for factor 7—Mogollon floristic element. 10, Distribution of species endemic to the southwestern United States. Isolines are labeled with the proportion of species in local floras occurring only in the study region.

all five floras in Table 7; the Western Durango flora shows low similarity with the same five floras. The Bavispe flora, in fact, shows significantly greater similarity with the Skull Valley flora at the western end of the Mogollon Rim region than it does with the Western Durango flora. These comparisons support an interpretation of factor 6 as an autochthonous element from the southwestern USA and northeastern Sonora. The Sierra Madre Occidental, like the Sierra Nevada and Rocky Mountains, might best be considered a floristic region separate from the Southwest region of this study. More floristic research in

Table 7. Comparison of selected southwestern floras with two floras from the Sierra Madre region of northwestern Mexico.

		Otsuka Similarity Index	
	Flora	Bavispe Region	Western Durango
21	Skull Valley Planning Unit	.262	.046
24	Sierra Ancha Experimental Forest	.349	.118
26	Saguaro National Monument	.459	.141
28	Chiricahua National Monument	.459	.145
29	Animas Mountains	.445	.136
	Western Durango	.172	—

northern Mexico is required to clarify relationships in this area.

7. Mogollon Element.—The last factor (Fig. 9) is centered in the mountainous region of central New Mexico, extending into Arizona along the Mogollon Rim, across the Kaibab Plateau, and onto the central Wasatch Plateau of southcentral Utah. This element is moderately correlated with the Rocky Mountain and Plains peripheral regions. The similarity with the Rocky Mountains region is largely due to species occurring in the southern Rocky Mountains. I have applied the designation "Mogollon" for this element because it centered about the Mogollon Rim of Arizona and the Mogollon Mountains of New Mexico.

Axelrod and Raven (1985) have recently reviewed the history of the Cordilleran Floristic Province, which they define as the Great Basin, Colorado Plateau, and Southern Rocky Mountains. They include the Mogollon area of this analysis in a Madrean Floristic Province. My analysis shows that the Mogollon area is more closely related to the Rocky Mountain region than to the Madrean region. Furthermore, the Great Basin area seems to have closer affinities with the northern Rocky Mountains than with the southern Rocky Mountains and Mogollon region. An analysis of a series of local floras situated throughout the Rocky Mountain region would be most helpful in resolving floristic relationships in the Cordilleran Region.

The maps of floristic elements can be combined to form a single map of floristic areas of the Southwest (Fig. 11), made simply by drawing lines around those floras sharing their highest loading with a particular factor. The position of a boundary between adjacent floras that lie in different floristic areas is determined by the relative magnitudes of the loadings between both floras and both factors. The map of floristic areas (Fig. 11) does not substitute for the maps of floristic elements. Like political units, floristic areas are two-dimensional whereas floristic elements, like representations of rainfall, temperature, or topography, are essentially three-dimensional. There is a one to one relationship between floristic elements and floristic areas in this analysis, but floristic elements are by no means confined to particular floristic areas.

The floristic areas recognized in this study are in close agreement with those of Dice (1943) for the Southwest. The only significant difference is that both my Colorado Plateau and Mogollon floristic areas would be included in Dice's Navahonian Biotic Province. The more recent treatment by Cronquist (1982) oversimplifies floristic relationships in the Southwest.

Reliability of the Analysis

Factor analysis is a nonhierarchical clustering technique that will produce clusters or factors from any data matrix. It is legitimate and important to question how accurately the factors depict the actual relationships among the variables. Does it produce the wrong clusters, or does it produce clusters when in fact none exist?

Unfortunately there are no simple statistical tests to answer these questions. I think there are two criteria that can be applied to factor analysis solutions. The first is that of interpretability. Stated simply, do the factors make sense? I have shown in the preceding section that the factors can be mapped directly to reveal their geographic meaning and that the particular factors arrived at correspond closely to floristic elements and areas in

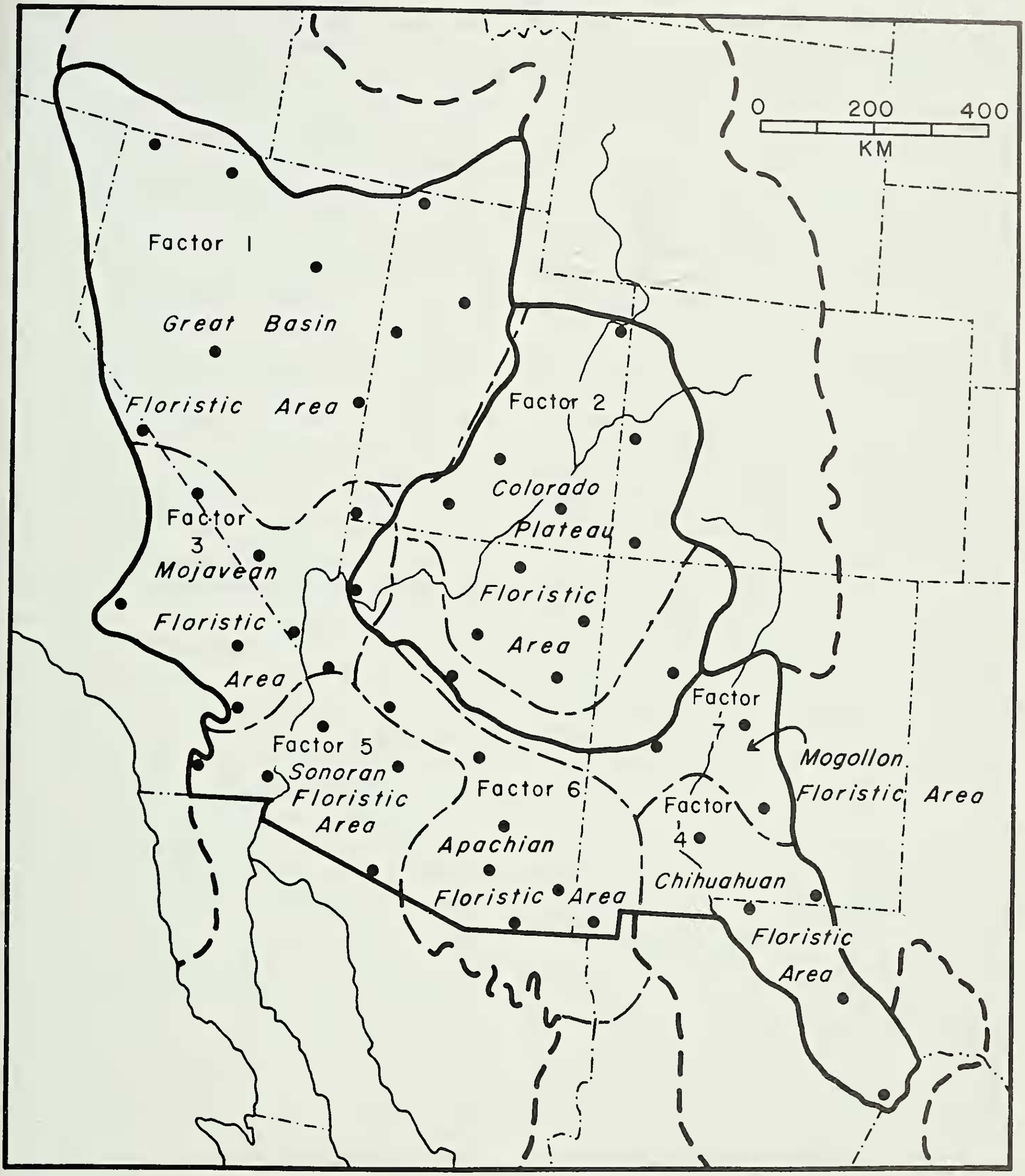


Fig. 11. Floristic areas of the southwestern United States identified from a factor analysis of similarity coefficients among 50 local floras.

the Southwest that have been recognized for at least 40 years. The factors found in this analysis are simply and sensibly interpretable.

The second criterion is that of consistency. If relationships among the variables are weak or if there are in fact no correlated clusters of variables, small changes in the factoring procedures or in the data are likely to result in substantial changes in the final solution. To check the consistency of the factor analysis solution, I made several changes in the data analysis and compared the results. Changes included using oblique rotation instead of orthogonal rotation, substituting Simpson's index of similarity (Simpson 1960) for Otsuka's, and omitting the checklists for the seven peripheral regions from the data base. Each of the alternative analysis produced a set of seven unipolar factors nearly identical to those depicted in Figures 3–9. The factor analysis solution does appear to satisfy the criterion of consistency.

Simpson's index did appear to be superior to Otsuka's index for use in this type of analysis. The communalities, defined as the sum of the squared factor loadings for each variable, measure the proportion of variance of each variable accounted for by the final factor analysis solution. With Otsuka's index the communalities were correlated with the size of the flora ($r = 0.43$, $p < .01$); with Simpson's index the communalities and flora sizes were not correlated ($r = 0.27$, $p > .05$). This means that the unexplained or residual variances were associated with the smaller floras using Otsuka's index. Intuitively it seems more reasonable either for the residual variance to be associated with the larger floras, or for it to be uncorrelated with flora size. Also, the final solution accounts for a larger proportion of the total variance (68.7%) when the similarities are expressed as Simpson's indices.

DISCUSSION

The flora of the Southwest can be described in terms of seven floristic elements. These elements can be objectively recognized and explicitly mapped. The derived maps (Figs. 3–9) show, however, not discrete units with clearly delineated boundaries, but rather geographic features varying in intensity from a central area of greatest development and diminishing gradually outward. Each element is most clearly developed in a limited area that can be characterized by topographic and climatic features that vary from adjacent areas dominated by other elements. Five of these areas—Great Basin, Colorado Plateau, Mojave Desert, Sonoran Desert, and Chihuahuan Desert—are widely recognized natural geographic areas. The other two—Apachian floristic area and Mogollon floristic area—are readily associated with upland regions separating adjacent lowland desert areas.

Floristic elements are objectively defined assemblages, but they are not discrete, bounded units in the sense of Clementsian formations or plant association types. Each of the 50 local floras used in the analysis contains representative species of several elements; likewise the species and elemental composition of the floras change in a continuous manner along geographic gradients. The situation is analogous to weather fronts and the particular state of the atmosphere at any particular time—the existence of continuous gradients in air pressure across a region is not contradictory to the recognition of high and low pressure cells in different areas of the region.

Somewhat surprisingly the analyses failed to recognize widespread elements. That is, there were no factors that could be associated with extensive groups such as "northern," "western," "boreal," "temperate," or "southwestern" areal types (Whittaker and Niering 1964). There certainly are widespread species, i.e., those of Table 4. Such species do constitute a significant fraction of any particular *local* flora, but they constitute a small fraction of the *regional* flora. The average extent of a floristic area in this analysis includes 7 floras, but the average range of a species includes only 4 floras. In fact, only 17% of the species of the region occur in 8 or more floras, beyond the average range of one floristic area, and only 6% occur in 15 or more floras, beyond the average range of two floristic areas. In many instances one could probably associate many of the subspecific taxa of the relatively few widespread species with specific floristic elements. No widespread elements were recognized because the factors reflect general trends among the ranges of the majority of species, which are not widespread.

The recognition of floristic elements, i.e., coincident patterns in species ranges, is not necessarily inconsistent with the individualistic concept of species distributions. The latter view states that no two species distributions are identical since each species has individual physiological tolerances and evolutionary history. Indeed, very few of the over 5,000 species occurring in the Southwest show an exact correlation of presence and absence in the local floras. The existence of floristic elements indicates that species have nonrandom, overlapping patterns of area, not that they are found consistently in similar communities, which is what the individualistic concept addresses. Many southwestern species are so uncommon that they may consistently occur together in similar areas, i.e., are members of the same local floras yet seldom or never occur together in the same community.

The problem of scale or scope is thus seen to be crucial in assessing the validity of associational concepts such as elements or assemblages of species. Whittaker (1970) presents graphs of overlapping, normal curves representing the abundances of dominant, woody species in local areas to argue against the existence of vegetation association types. The quadrats or plots of the ecologist, however, contain only a minute fraction of a regional flora. As one expands the sample area from plots to local floras to floristic areas, the "grain" in species composition becomes finer and patterns emerge. At the scale of continents, I doubt that any biogeographer fails to recognize the existence of distinctive biotas.

The best explanation for groups existing at regional levels while continuity prevails at local levels involves barriers to migration. Such barriers are largely lacking for terrestrial plants at the level of quadrats and plots, but they become more common and more effective as one increases scale. At the level of continents oceans provide very effective barriers to migration; at the level of floristic areas topography and climate provide sufficiently effective barriers to promote regional differentiation of the flora into floristic elements. Important barriers in the Southwest that serve to segregate one or more floristic elements include the Mogollon Rim along the southern boundary of the Colorado Plateau, the Wasatch Plateau in central Utah, the highlands of southeastern Arizona and southwestern New Mexico (including the rather low-lying continental divide in this area), and the broad zone of increasing basal elevation in southern Nevada.

Migration has been depicted in the literature as a process that should effectively preclude the formation or recognition of floristic elements. Gleason (1926) argued that both individualistic tolerances and extensive migrations of species were inconsistent with the recognition of recurring associations of species. Good (1931) and Mason (1936) elevated to a "principle" the assertion that extensive migrations of *floras* had occurred in the past. Gleason and Cronquist (1964) stated that *most* plant species are capable of migrating to all suitable habitats and that such migrations are sufficiently rapid to keep pace with environmental changes. How then can floristic elements be maintained in the face of such extensive migrations?

The fact is that observed patterns of plant distributions in the Southwest do not provide much evidence of extensive migration as a general phenomenon. The uncommonness of the majority of species indicates either that most plants are rather poor migrators or that insufficient time has elapsed for these species to complete their migrations. Both are probably true for southwestern species.

Two observations seem to support the view that plants can and do migrate to nearly anywhere within the range of their physiological tolerances. First, many (but not all) seeds and fruits do possess obvious adaptations for dispersal. Second, the fossil record provides concrete evidence that some species have migrated widely. Nevertheless, from these observations it does not follow that all or most plant species actually have migrated extensively.

Migration is a matter of probabilities. The vast majority of seeds dispersed by plants travel very short distances (Levin and Kerster 1974). The occasional long-distance transport of a single seed or fruit is unlikely to result in successful colonization within a stable, competitive community. Most importantly, the likelihood of successful migration is dependent on the number of seeds of the species dispersed per unit of time compared to other potential migrators. The majority of plant species in the Southwest occur in three or fewer local floras and may simply not be abundant enough to generate a flux of seed sufficiently great to make extensive migration likely, even over considerable spans of time.

Most of the actual examples of extensive migration in the fossil record involve dominant, usually woody species. These plants constitute a small fraction of the southwestern regional flora. Derivation of general principles for all species of plants from data on the current and former distributions of species such as redwoods, sugar maples, and other forest trees is a questionable practice that may have led to some unwarranted conclusions.

If the capacity of most species to migrate to all areas suited to their physiological tolerances were as pervasive as typically assumed, I would expect the average range of a species to be much wider. One could argue that species in the Southwest have very narrow physiological tolerances that effectively restrict them to relatively few habitats within a limited area, but that seems rather unlikely given the similar nutritional needs of plants and the apparent lack of coincidence between most species and very specific habitats. It seems much more likely that barriers to migration, competition, and low rates of seed dispersal interact to greatly curtail the ability of most species to migrate.

Over the past several years a general model of southwestern phytogeographic history has emerged that includes several postulates: (1) most species present today had evolved by the end of the Tertiary, (2) these species have undergone extensive and intensive migrations in response to Pleistocene climate changes, and (3) modern plant distributions reflect both this migrational history and the tolerances of species for modern climatic conditions.

The concept of great species longevity is supported by Levin and Wilson (1976), who estimated the mean duration for herbaceous species to be 10 million years, with a mean speciation rate of 1.15 lineages per million years. Woody species were estimated to be even more persistent and to have even slower rates of speciation. Consistent with this view, Tidwell et al. (1972) hypothesized that the flora at the beginning of the Pleistocene in the Intermountain Region was basically the same as exists today.

The best evidence that many dominant species have indeed undergone extensive migrations in the Southwest at the end of the Pleistocene comes from fossil packrat middens (Van Devender and Spaulding 1979, Wells 1983). Many workers have textraploted these results back to previous glacials and interglacials, concluding that the repeated climate changes occurring during the Pleistocene in topographically heterogeneous intermountain environments would have kept species populations in constant movement (Cronquist 1978).

It is difficult to conceive how recognizable floristic assemblages could survive through the Pleistocene with all this movement, fluctuation, and shuffling of populations in response to climate change. My analysis of modern plant distributions in the entire regional flora, however, casts some doubt on the generality of the consensus model outlined above. Most of the local floras included in this analysis are from areas encompassing extensive elevational relief. Southwestern mountain ranges, particularly in the Basin and Range Province, possess considerable habitat diversity in association with elevation, typically going from desert at the base to pinyon-juniper woodland, pine forest, or even spruce forest at the top (e.g., Lowe 1964). Old species with extensive migrational histories would have left relictual populations scattered within and between these ranges. Only a single, small population is required to establish a species as a member of a local flora. The consensus model would predict that the ranges of most species would include many such scattered, relictual populations, resulting in a modern flora with most species widely distributed throughout the region and little differentiation of the floristic assemblages within the region.

Many species, particularly those of high elevations, do show distribution patterns consistent with the consensus model, but they do not constitute a large fraction of the Southwest flora. For the rare species consisting of small populations in only a few floras, i.e., the majority of species in the Southwest today, extinction, rather than migration, is the more likely response to severe climate change. These species are unlikely to possess sufficient ecotypic, genetic diversity or sufficiently large populations required to keep pace with the changing environment.

Speciation, however, may also be accelerated during periods of severe climate change (Stebbins 1947, Axelrod 1981). Many southwestern species probably originated in postglacial time in response to the new, more arid environments created by the changes from Pleistocene to Holocene climates. Such an interpretation has been applied to *Atriplex* (Stutz 1978) and seems likely for many of the species of large southwestern genera such as *Eriogonum, Astragalus, Penstemon, Gilia, Camissonia, Cryptantha, Phacelia, Opuntia,* and others.

Do we need two models of evolutionary response to climate change, one for common species and one for rare species? I think not. Common plant species consist of many populations of subspecies, varieties, or ecotypes. During periods of severe climate change, some of these ecotypes will migrate, many will go extinct, and some will differentiate to form new ecotypes, varieties, subspecies, and species in new habitats. As a result, the range of the species before the climate change (i.e., in the fossil record) will be different from its range after the climate change. But migration of populations or ecotypes existing before the climate change and persisting through the climate change need account for only part of the total change in the range of a species. In other words, the most likely response of any particular small population to rapid environmental change is extinction; the probability of a species becoming extinct depends in large part on how many populations it has.

The seven floristic elements identified in the present analysis are clearly associated with modern, Holocene environments. They represent centers of postglacial differentiation and speciation within the depleted flora surviving at the end of the Pleistocene in the Southwest, partially but effectively isolated from adjacent elements by modern climatic and topographic barriers.

My analysis of specific similarities among local floras of the Southwest is consistent with a hypothesis of Holocene differentiation of the modern regional flora. An analysis of generic similarities among these floras might better reflect the Tertiary and Pleistocene migrational history of the flora, since the majority of the genera are doubtless of Tertiary age. My interpretation of the evolution of the southwestern flora is also consistent with the concept of punctuated equilibria, as opposed to slow, gradual phylogenetic change, which would be more consistent with the consensus model discussed above.

American plant ecology has been very much a science of dominants. This bias has been carried over into plant geography, which has emphasized the distribution of vegetation almost to the exclusion of flora. I have tried to show in this paper how a study of the entire flora of a region, weighing all species equally, can reveal patterns that may not follow from or be in agreement with principles and models derived solely from study of the dominant species. Floristics and vegetation analysis are complementary approaches to understanding the distribution and abundance of plants. Phytogeography needs both.

Acknowledgments

I thank R. M. Turner, J. H. Brown, J. E. Bowers, and M. A. Kurzius for reading and commenting on the manuscript. M. Beauchamp, J. E. Bowers, D. Clemons, R. A. Fletcher, T. R. Van Devender, and R. D. Worthington helped in the acquisition of floras and unpublished checklists. The illustrations were prepared by M. A. Kurzius.

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